

Emerging opportunities and challenges in phenology: a review

JIANWU TANG,^{1,†} CHRISTIAN KÖRNER,² HIROYUKI MURAOKA,³ SHILONG PIAO,^{4,5} MIAOGEN SHEN,⁵
STEPHEN J. THACKERAY,⁶ AND XI YANG⁷

¹*Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA*

²*Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland*

³*River Basin Research Center, Gifu University, 1-1 Yanagido, Gifu 501-1193 Japan*

⁴*Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871 China*

⁵*Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, CAS Center for Excellence in Tibetan Plateau Earth Sciences, Chinese Academy of Sciences, 16 Lincui Road, Chaoyang District, Beijing, China*

⁶*Lake Ecosystems Group, Centre for Ecology & Hydrology, Lancaster Environment Centre, Bailrigg, Lancaster LA1 4AP UK*

⁷*Department of Earth, Environmental and Planetary Sciences, Brown University, Providence, Rhode Island 02912 USA*

Citation: Tang, J., C. Körner, H. Muraoka, S. Piao, M. Shen, S. J. Thackeray, and X. Yang. 2016. Emerging opportunities and challenges in phenology: a review. *Ecosphere* 7(8):e01436. 10.1002/ecs2.1436

Abstract. Plant phenology research has gained increasing attention because of the sensitivity of phenology to climate change and its consequences for ecosystem function. Recent technological development has made it possible to gather invaluable data at a variety of spatial and ecological scales. Despite our ability to observe phenological change at multiple scales, the mechanistic basis of phenology is still not well understood. Integration of multiple disciplines, including ecology, evolutionary biology, climate science, and remote sensing, with long-term monitoring data across multiple spatial scales is needed to advance understanding of phenology. We review the mechanisms and major drivers of plant phenology, including temperature, photoperiod, and winter chilling, as well as other factors such as competition, resource limitation, and genetics. Shifts in plant phenology have significant consequences on ecosystem productivity, carbon cycling, competition, food webs, and other ecosystem functions and services. We summarize recent advances in observation techniques across multiple spatial scales, including digital repeat photography, other complementary optical measurements, and solar-induced fluorescence, to assess our capability to address the importance of these scale-dependent drivers. Then, we review phenology models as an important component of earth system modeling. We find that the lack of species-level knowledge and observation data leads to difficulties in the development of vegetation phenology models at ecosystem or community scales. Finally, we recommend further research to advance understanding of the mechanisms governing phenology and the standardization of phenology observation methods across networks. With the opportunity for “big data” collection for plant phenology, we envision a breakthrough in process-based phenology modeling.

Key words: cameras; greenness; ILTER; modeling; phenology; scale; Special Feature: International LTER.

Received 3 November 2015; revised 28 April 2016; accepted 26 May 2016. Corresponding Editor: K. Vanderbilt.

Copyright: © 2016 Tang et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** jtang@mbi.edu

INTRODUCTION

Plant phenology, the study of recurring events in the life cycle of plants, has gained increasing public and scientific attention over the last few

decades. Since 1980, the number of peer-reviewed journal articles related to plant phenology has increased by about 10-fold (Fig. 1). The rejuvenation of this long-studied subdiscipline of ecology has been primarily induced by three factors: (1)

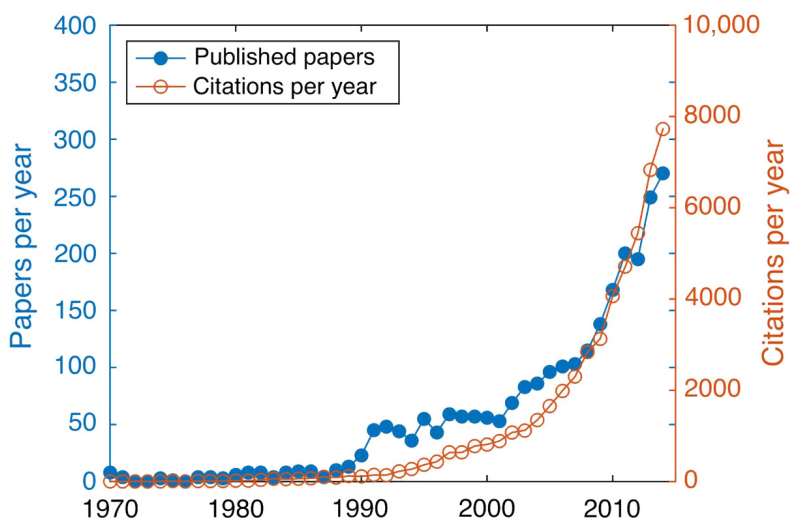


Fig. 1. Trends of papers and citations of vegetation phenology each year between year 1970 and 2014. The statistics are from an ISI Web of Knowledge search conducted on 26 October 2015 using the following terms: (Title = Phenolog*) AND (Topic = vegetation OR Topic = plant).

phenological shifts are a ubiquitous phenomenon and can be interpreted as a sensitive indicator of the ecological impacts of climate change (Walther et al. 2002); (2) the consequences of phenological shifts, including the start, senescence, and the duration of growing seasons, significantly impact ecosystem structure and function, such as leaf area, photosynthesis, carbon cycling, and species composition and competition, but the mechanistic understanding of these links and feedbacks to climate change is currently incomplete (Richardson et al. 2012); and (3) technological developments, particularly in remote sensing and near-surface observation, have radically expanded the scale of phenological observation beyond traditional manual observation (Zhang et al. 2003, Richardson et al. 2009, Yang et al. 2012, 2014). Despite these advances, a deeper mechanistic understanding of phenology, its variability and drivers across multiple scales, and its link to other physiological processes is still needed. The lack of this fundamental understanding has limited our ability to develop predictive models (Basler 2016).

Integration of multiple disciplines, including ecology, evolutionary biology, and climate science, with remote sensing and long-term, high-frequency monitoring data across multiple spatial scales is essential to advance phenological research. Although the word “phenology” originates from Greek φαίνω (phainō)—to show and

to bring to light—referring to visible changes in biological development, modern phenological research should go beyond visible observation of biological events by looking deeply into the physiological mechanisms of these changes. Plants change the timing of leaf-out, leaf senescence, and flowering according to environmental cues, for example, temperature (Richardson et al. 2006, Vitasse et al. 2011), irradiance (Saleska et al. 2007), precipitation (Craine et al. 2012, Shen et al. 2015), and photoperiod (Körner and Basler 2010, Basler and Körner 2012). These cues or drivers may vary in importance at different scales, depending on species, biomes, and environmental constraints. Therefore, lessons learned or models built from one species or ecosystem may not be widely applicable unless we possess the mechanistic insight to permit generalizations for other systems. The variation in these responses to a changing climate could be traced to genetic controls and evolutionary processes in addition to the environmental drivers (Wilczek et al. 2009). Phenology could also exert feedbacks to the climate system through changing leaf structure, energy balance, and carbon and water cycles (Penuelas et al. 2009). An integrated framework is urgently needed to advance our understanding of the mechanisms driving phenological shifts and their consequence on ecosystem structure, function, and biogeochemical cycles (Wolkovich et al. 2014).

The study of phenology spans multiple spatial and ecological scales, each with its own suite of observational methods. While genetic tools have been used to understand the controls over flowering in model plants such as *Arabidopsis thaliana* (Chew et al. 2012, Satake et al. 2013), a search of the current literature (using the ISI Web of Knowledge) suggests that most studies focus on broader ecosystem scales, with remote sensing being one of the most frequently used tools. Satellite remote sensing provides data on total vegetative growth (usually using indices like the normalized difference vegetation index [NDVI]) on a daily or weekly basis over large areas (e.g., Fisher and Mustard 2007, Xu et al. 2013). Recently, the development of near-surface remote sensing techniques, such as digital repeat photography or spectroscopic sensors, has provided high-temporal-resolution (~hourly) data of vegetation activities. On the other hand, long-term ground observations, especially of some dozen-year-old or hundred-year-old historical data (Miller-Rushing et al. 2006), are still valuable and complementary to newer technologies as the former provides phenological data of individual plants and species often over a longer time period than those of available satellite or repeat photography data. The above three methods—in situ ground observations, near-surface, and remote sensing—continue to provide rich data from multiple spatial scales and also opportunities to transfer mechanistic understanding from detailed local studies to the development of quantitative models.

The scope of phenology studies across time and space requires long-term research and international collaboration. For example, recording the interannual variation in leaf-out dates is essential to understanding the environmental cues of leaf-out. Without years of leaf-out data across species, ecosystems, and biomes, we will not be able to generalize the responses of spring phenology to environmental change and, therefore, to predict the impact of future climate change. The International Long Term Ecological Research network (ILTER), a global network of approximately 600 research sites located in diverse ecosystems, plays a unique role in providing existing long-term phenology data across biomes and regions. The ILTER could also serve as a powerful mechanism for the standardization of future phenology data collection using new technologies to advance phenological research.

In this review, we briefly revisit the mechanisms and drivers of plant phenology as a foundation for guiding future technological advancement and model development. Then, we summarize recent advances in observation techniques across multiple spatial scales using examples drawn from ILTER sites. Finally, we review phenology models as an important component in earth system modeling. We close with recommendations for future research directions in phenology, emphasizing the importance of long-term, multidisciplinary research.

MECHANISMS AND DRIVERS OF PLANT PHENOLOGY

Plant phenology responds sensitively to the changing environment for two general reasons: (1) to achieve synchrony in sexual reproduction among individuals of a given population (gene flow) and (2) to escape unfavorable seasons in a precautionary way. While the first can use any environmental signal, all individuals of a population have evolved as a result of the second reason, which requires signals to avoid exposure of unhardened or fragile tissues to damaging environmental conditions such as freezing temperatures. As concurrent weather is an intrinsically unreliable predictor of extreme events, plant evolution in temperate climates has selected for the perception of signals that bear, in a probabilistic manner, a minimum likelihood of fatal exposure to extremes. Although not fully understood, it is clear that most species in temperate climates adopt a mix of signals that fall into three categories: (1) solar signals (photoperiod), (2) past seasonal experience signals (winter chilling), and (3) current or very recent past signals (concurrent temperature and/or water conditions). When photoperiod is employed for spring phenology, winter chilling must be employed as well, because day length is the same in spring and autumn and thus the legacy of winter experience (chilling exposure) is needed to sensitize plants to spring or autumn (Schwartz and Hanes 2010, Polgar and Primack 2011). Alternatively, plants may solely rely on thermal forcing, as winter transitions to summer. However, the temperature signal is less reliable because exceptionally warm early spring weather may induce leaf-out before the statistical risk of freezing is over (i.e., a “false spring”; Allstadt

et al. 2015) or rainy season begins (Shen et al. 2015). Whatever combination of signals plants utilize, the influence of concurrent temperature will force development, once the internal requirement has been met (Körner and Basler 2010).

Different life history strategies among plants will select for less or more precautionary phenology. In spring, short-lived, highly reproductive, so-called *r*-strategists will more likely adopt an opportunistic phenology (in the extreme case just following concurrent temperature), whereas long-lived, slowly reproducing plants (*K*-strategists) such as late-successional forest trees will adopt a strategy that ensures century-long life (Pianka 1970, Steltzer and Post 2009, Körner and Basler 2010, Wolkovich et al. 2014). Opportunistic plants may lengthen their growing season in warming springs, but late-successional, low-risk plants may take less advantage from a warmer spring. Hence, there is a trade-off between freezing tolerance and required season length that defines the distributional range of species that adopt different phenological strategies (Lenz et al. 2014, Vitasse et al. 2014a, b, Körner et al. 2016).

In autumn, the late season transition to dormancy should occur before the advent of periods that bear a risk of freezing damage. Most temperate and boreal trees use photoperiod as a reliable signal for the onset of autumnal hardening. Yet, unlike spring phenology that can be visually observed clearly (e.g., budbreak and leaf flushing), autumnal phenology cannot be readily assessed by visual signals. Leaf coloration in autumn is only a final step of a cascade of invisible developmental processes (such as winter bud set or leaf abscission layer formation), most commonly induced by unpredictable cold nights. Hence, satellite images, automated systems, or phenology modeling is intrinsically limited to assess “true” autumn phenology (Yang et al. 2012), because data on canopy color change do not tightly relate to the underlying processes of phenology in autumn (Körner et al. 2016).

In addition to the above abiotic cues, biological factors, including competition, resource limitation, and genetics, also control phenology, particularly during the period of a stable environment (Wolkovich et al. 2014). Coexistence of species in a community often demonstrates a similar phenological pattern of each species under the similar

climatic condition by minimizing competition. The genetic control of phenology limits the plasticity of phenological shifts and protects a species or population from climate extremes. For example, when the southern and northern populations of *Eriophorum vaginatum*, a dominant species in the arctic tundra, were transplanted to a central location in the Toolik Station in Alaska, an ILTER site, the dates of senescence of each population remained unchanged (i.e., northern population senesced earlier than the southern one despite the shift of temperature and photoperiod), indicating a genetic control of phenology for each population (T. Parker, J. Tang, M. Moody, and N. Fetcher, *personal communication*). Therefore, to fully understand phenology and its response to the changing climate, abiotic and biotic drivers should be differentiated and integrated into modeling efforts (Steltzer and Post 2009, Schwartz and Hanes 2010, Pau et al. 2011, Wolkovich et al. 2014). Insights from these studies can be used to guide the technological development of phenological observation (e.g., using high-resolution near-surface and remote sensing data to differentiate phenological differences across species that may respond differently to environmental drivers) and the experimental design (e.g., using warming and transplanting experiments to detect abiotic and biotic drivers of phenology).

PHENOLOGICAL STRATEGIES AND CONSEQUENCES

The complexity of biodiversity and multiple controls of plant phenology result in highly variable responses of plant phenology to climate among species, communities, and ecosystems (Rollinson and Kaye 2012, Shen et al. 2014a). There are four broad phenological strategies with which plants respond to the environment. (1) Opportunistic species: *r*-selected species, as described above, for which leaf-out in spring is less precautionary as it follows direct thermal forcing. (2) Strict species: *K*-selected species as described above that employ stronger photoperiodic controls than opportunists. (3) Exotic species: exotic plants that are not adapted to their “new” climates. For example, orchard trees planted in humid-temperate climates, including apricot (*Prunus armeniaca*), cherry (*Prunus avium*), and apple (*Malus domestica*), have an

evolutionary heritage from central or central-west Asia, with a very continental climate and abrupt and reliable onset of spring (Janick 2005). Hence, it is common in the orchard industry that plants suffer from frost after leaf-out in response to the conditions typical of an unpredictable spring. (4) Ornamental species: ornamental plants that exhibit extreme forms of opportunistic phenology in response to temperature, because they originate from regions with hardly any freezing risk and almost behave like a biological thermometer, advancing their phenology by accumulating degree-days (Defila and Clot 2001). Examples are horse chestnut (*Aesculus hippocastanum*) and lilac (*Syringa vulgaris*; Larcher 2006).

Given these different phenological strategies, observations obtained from one of the above groups may not necessarily apply to other groups. Phenology patterns found in ornamental trees, domestic trees, exotic taxa, and more generally ruderal/pioneer taxa may not be fully applicable to late-successional forest trees. This species variation in the strategy to respond to climate should be considered when designing monitoring strategies and also developing models to capture generic responses to environmental change.

Species within a plant community will likely not respond to climate change using the same phenological strategies, which may have significant consequences for resource (i.e., light and nutrients) competition, food webs, ecosystem productivity, carbon cycling, and other ecosystem functions and services. Within the plant community, responses of canopy trees and understory shrubs and herbs to climate change may affect competition of these functional groups for spring light and soil nutrients (Vitasse 2013), and thus the overall ecosystem production and carbon cycling. Cross-species variation in phenological responses to climate change can also cause mismatch and disrupt the synchrony of species interactions. For example, under global warming during the 1975–2000 period, winter moth (*Operophtera brumata*) eggs hatched earlier than oak (*Quercus robur*) bud burst in the Netherlands, profoundly affecting population dynamics of the winter moth (Visser and Holleman 2001). Advanced observational technologies, coupled with long-term human-collected data

measuring shifts in phenology, can be a powerful combination for better understanding the mechanisms that cause changes in phenology and their ecological consequences.

ADVANCEMENT OF MEASUREMENT METHODS AND LONG-TERM DATA

To advance understanding of the above phenological mechanisms, drivers, strategies, and their variations among species will require extensive, intensive, and long-term measurements of phenological data. Multiscale, long-term phenological monitoring allows interpretation of the mechanisms behind observed phenology. The metrics for plant phenology measurements include budbreak, leaf expansion and maturation, flowering time, senescence (coloring), and leaf abscission. The methodology for such observations includes the recording of phenological events by eyes, periodic photography, automatic repeat photography, and satellite-based remote sensing (Morissette et al. 2009). During the past decades, the leaf and canopy phenology of vegetation has been focused on remote sensing observations from a single research plot to regional, continental, and global scales to detect any phenological changes due to interannual variation in climatic conditions or ongoing global warming (Cleland et al. 2007, Richardson et al. 2007, Piao et al. 2008, 2015). During the last decade, camera-based observations have been popular with the advancement of digital repeat photography (Richardson et al. 2007, 2009, Ide and Oguma 2010, Nagai et al. 2011). In addition, spectroradiometers have become powerful tools to monitor the spectral reflectance of both individual leaves and whole canopies (Asner and Martin 2008). Such data can be compared with the reflectance measured by satellite-based remote sensing (Muraoka et al. 2013b) and with laboratory assays of leaf traits (Yang et al. 2014) that provide physiological information otherwise invisible when solely recording reflectance of visible bands.

In the following sections, we summarize the recent advancement of methodologies for long-term monitoring of leaf and canopy phenology at multiple spatial scales. The methods and techniques used by satellite-based remote sensing have been widely reviewed elsewhere (e.g., Zhang et al. 2003, Homolova et al. 2013).

Digital repeat photography

With the advancement of commercial digital cameras, time-lapse cameras have become a widely used tool to monitor temporal changes in plants and the landscape. To observe terrestrial vegetation and its structure and function, and to link to remote sensing data from satellites, sensor networks, including “PhenoCam” (<http://phenocam.sr.unh.edu/webcam/>), “European Phenology Network (EPN),” and “Phenological Eyes Network (PEN)” (<http://www.pheno-eye.org/>), were established in multiple sites across forests,

grasslands, and paddy fields (Richardson et al. 2009, Motohka et al. 2010, Nasahara and Nagai 2015). Camera-based phenology measurements allow direct observation of terrestrial vegetation from diverse habitats across the world and provide data that can be linked with measures of ecosystem structure and functions. These cameras are currently located in many long-term ecological and carbon flux sites such as the AmeriFlux (<http://ameriflux.lbl.gov/>), NEON (National Ecological Observatory Network of the United States; <http://www.neoninc.org/>), EUROFLUX, AsiaFlux

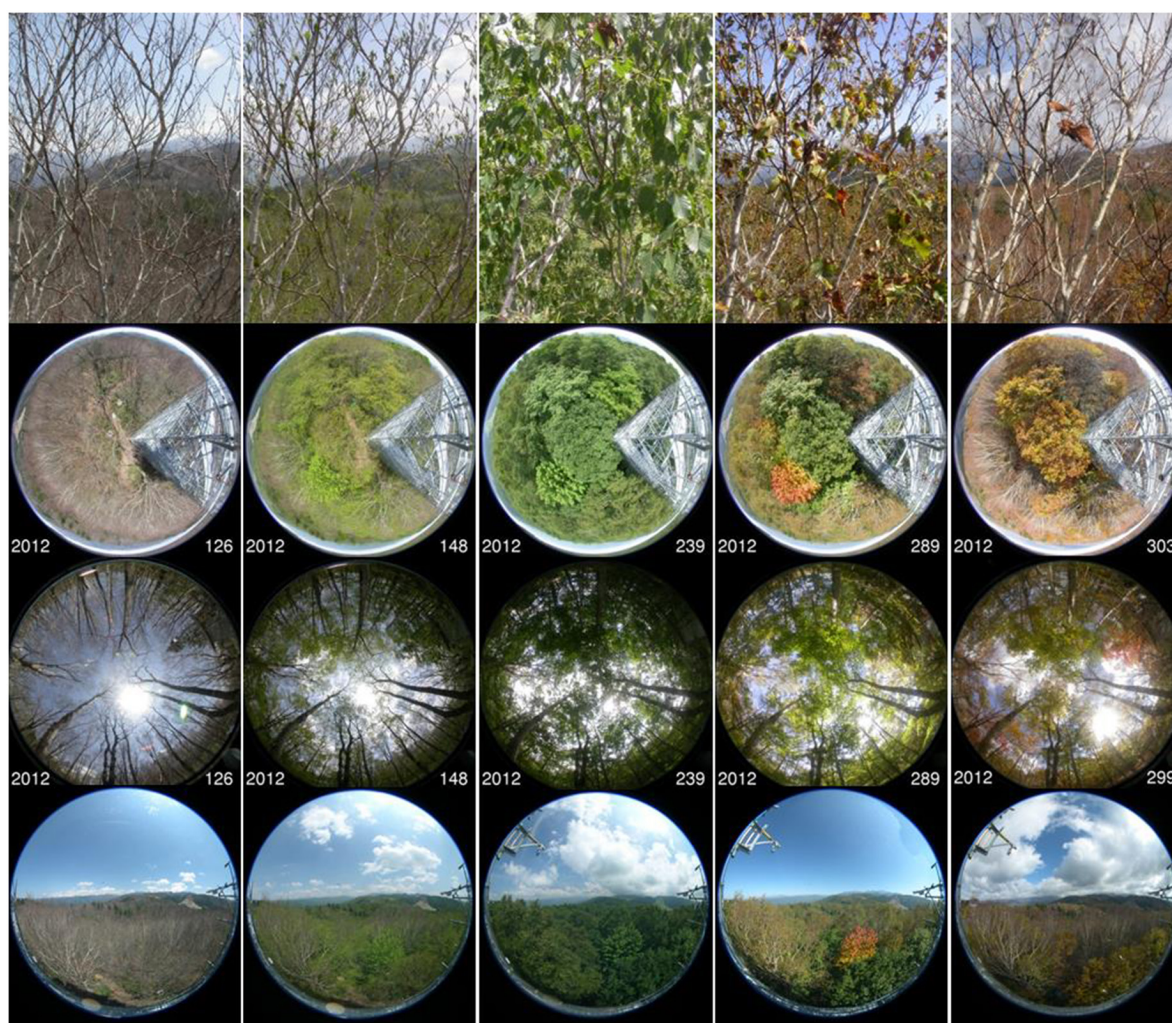


Fig. 2. Examples of digital repeat photography at the Takayama site (a JaLTER site, part of the ILTER) by the PEN camera systems. From the top to the bottom: branch of *Betula ermanii*, a canopy tree; downward view of the canopy; upward view of the canopy; landscape surrounding the forest. From left to right: early spring before leaf emergence; leaf expansion in late spring–early summer; canopy maturation in mid-summer; leaf coloring in autumn; leaf fall in late autumn.

(<http://asiaflux.net/>), JaLTER (Japan Long Term Ecological Research network; <http://www.jalter.org/>), CERN (Chinese Ecological Research Network; <http://www.cern.ac.cn/>), LTER (Long Term Ecological Research network of the United States; <http://www.lternet.edu/>), and other ILTER (International Long Term Ecological Research network; <http://www.ilternet.edu/>) sites as an integrated element of measured variables. Many of these data are now accessible online. Networks such as these have an important role to play in providing comparable phenological data across ecosystems within each network. Calibration of cameras to make them interoperable across the networks is strongly needed (Wingate et al. 2015) to facilitate internetwork data comparisons.

Within these networks, digital cameras for repeat photography are mounted on observation towers to monitor leaf, branch, canopy, and landscape phenology. The cameras can be set to take pictures downward from the tower, upward from the ground, horizontally, or with fisheye views (Fig. 2). Fisheye images have been used to take hemispherical canopy photographs for estimating the light environment of the forest understory (Anderson 1964, Chazdon and Field 1987, Pearcy 1989) and forest canopy leaf area index (LAI; Jonckheere et al. 2004). With the automation of repeat fisheye images, continuous LAI data at the canopy scale are available. In addition, species-level observation with cameras has also been reported (Nijland et al. 2014).

Image processing

Images taken by digital cameras contain values of red (R), green (G), and blue (B) as “spectral band” signals to detect the characteristics of the observed objects. For example, Richardson et al. (2007) and Nagai et al. (2011) examined the RGB signals as an indicator of phenological status of deciduous broadleaf forest canopies, and Saitoh et al. (2012) collected such data for an evergreen coniferous forest canopy, both confirming the capacity of this method to quantify canopy structure (LAI) and function (photosynthetic capacity, leaf chlorophyll content, or eddy-covariance-based gross primary production).

The RGB data are converted to greenness indices to quantify the seasonal change, either as the green excess index (GEI; Richardson et al. 2007, Saitoh et al. 2012, Nagai et al. 2014) or as

the green chromatic coordinate (Gcc; Sonnentag et al. 2012). GEI and Gcc are calculated as:

$$\text{GEI} = (G - R) + (G - B) = 2G - (R + B); \quad (1)$$

$$\text{Gcc} = G / (R + G + B); \quad (2)$$

where G is the green digital number from image files, R is the red digital number, and B the blue digital number.

These indices are widely used as a proxy to describe phenological patterns across the season, either in a natural environment or in warming experiments to detect phenological shifts in response to experimental warming (e.g., Chung et al. 2013). However, recent findings indicate that the camera-based greenness indices may not reveal leaf physiology that ties closely with photosynthesis (Yang et al. 2014, Liu et al. 2015). For example, Yang et al. (2014) found that the camera greenness peaked 20 days earlier than the peak of leaf chlorophyll and carotenoids that are a better proxy for photosynthesis, and the decline of the greenness after the spring peak detected from cameras may not reflect the real change of the LAI. Further development of greenness indices or corrected indices that fully use visible-band camera images or expand the visible bands to broader bands is needed to reveal seasonality of physiological traits of plants.

Other optical measurements

Visible-band images obtained from digital cameras could be expanded to other complementary optical measurements to reveal more physiological and functional traits of plants. For example, to estimate gross primary production, one needs to know both the growing season length, which can be monitored by camera-based phenology, and photosynthetic rates. The latter could be directly measured by a photosynthesis system (e.g., LI-6400; LI-COR, Lincoln, Nebraska, USA), or estimated by a proxy, such as the leaf chlorophyll content. Chlorophyll contents are correlated with photosynthetic capacity of leaves throughout the seasons (Noda et al. 2015) and could be detected by measuring absorption of certain wavelengths by extracts of leaf pigments (Porra et al. 1989, Gitelson et al. 2003). The “SPAD meter” (Konica Minolta, Osaka, Japan) has been used to monitor the leaf chlorophyll content. The SPAD meter contains two light-emitting diodes

for 650 and 940 nm, and a photodiode detector measures the transmittance of red and infrared light (Markwell et al. 1995). The SPAD values have to be validated against chlorophyll content data, extracted from the leaves to convert the values to chlorophyll contents (Markwell et al. 1995). Simultaneous measurements of SPAD and leaf photosynthetic capacity are useful to investigate the phenology of the leaf physiological status over the season (Muraoka and Koizumi 2005, Liu et al. 2015). In addition, by combining with the RGB information obtained by a digital camera, SPAD values provide insights into the eco-physiological background of seasonal changes of canopy color (Nagai et al. 2011, Liu et al. 2015).

To quantitatively measure the leaf expansion within the canopy over the season, optical properties at the canopy scale, either reflectance or transmittance, could be recorded to capture the foliage and branch optical properties (Verhoef 1984). The seasonality of leaf expansion can be monitored by measuring the transmittance of photosynthetically active photon flux density above and below the canopy with light sensors to estimate LAI (Pearcy 1989, Hirose 2005, Monsi and Saeki 2005, Tang et al. 2008). In addition, the spectral reflectance of the canopy recorded by a spectroradiometer that covers wavelengths beyond the visible bands of the solar spectrum can be used to estimate the structural and biochemical conditions of the canopy, for example, as the NDVI. The spectral reflectance data and vegetation indices obtained by satellite remote sensing (Piao et al. 2003, Motoshka et al. 2010, Muraoka et al. 2013b) have been used to monitor physiological characteristics of vegetation such as pigment contents, leaf nitrogen, and water contents (Nakaji et al. 2007, 2008, Hilker et al. 2010, Asner et al. 2014, Stagakis et al. 2014, Yang et al. 2014).

Solar-induced fluorescence

Solar-induced chlorophyll fluorescence (SIF) has emerged in recent years as a new tool to monitor beyond “visible” leaf color by focusing an “invisible” ecosystem function, that is, photosynthesis (Joiner et al. 2011, 2013, Yang et al. 2015). SIF is a by-product of photosynthesis: When CO₂ is assimilated under sunlight, a small fraction of solar energy (<1%) captured by chlorophyll is emitted as fluorescence at a longer wavelength (650–800 nm; Baker 2008, Meroni et al. 2009). SIF could

be proportional to photosynthetic rates, and thus act as a proxy of photosynthesis at various scales. However, recording the fluorescence signal is extremely difficult because the weak radiation is obscured by the much higher intensity of solar radiation and its reflection from plants. Fortunately, because of the existence of a few absorption bands at which the atmosphere absorbs the solar radiation, for example, at the oxygen absorption wavelengths at 687 and 760 nm, measuring the very weak signal of fluorescence is possible (Daumard et al. 2010, Guanter et al. 2013). With the newly launched satellites GOSAT (Greenhouse Gases Observing Satellite), GOME (Global Ozone Monitoring Experiment) 2, and OCO (Orbiting Carbon Observatory) 2, we are able to monitor fluorescence across the globe, and potentially derive GPP and analyze the controlling factors and effects of stresses across space and time (Joiner et al. 2011, Guanter et al. 2012, Lee et al. 2013). More recently, ground-based SIF has been continuously monitored and found to have a strong correlation with GPP measured from an independent method (the eddy-covariance method) at Harvard Forest, an ILTER site (Yang et al. 2015), showing a great potential of using SIF to advance understanding of phenology and other ecosystem functions.

Spatial scales: leaf, plot, regional, and global

Phenology observations over a range of spatial and temporal scales are required to detect plant and ecosystem responses to changing environmental conditions (e.g., Cleland et al. 2007, Chung et al. 2013, Richardson et al. 2013). Leaf-scale phenology may not match canopy-scale phenology as the light conditions and nutrient supplies of leaves vary across the canopy height (Hirose 2005). Moreover, scaling canopy phenology to the region and the globe is challenging because species composition plays an important role at such larger scales and different species may respond differently to changing environmental conditions as summarized in earlier sections.

Relationships between leaf ecophysiological characteristics and optical properties at smaller scales, from the single leaf, tree crown to forest canopy, have been used to estimate phenological changes at broader spatial scales from the landscape to regions, continents, and the globe (Muraoka and Koizumi 2009). This approach has

been introduced to ILTER-EAP (East Asia–Pacific regional network of ILTER) and J-BON (Japan Biodiversity Observation Network; Muraoka et al. 2013a). Vegetation indices obtained from satellite-based remote sensing data such as MODIS (Moderate Resolution Imaging Spectroradiometer) have been validated with ground-based data. The following vegetation indices have been introduced:

$$\text{NDVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R}), \quad (3)$$

$$\text{EVI} = 2.5(\text{NIR} - \text{R}) / (\text{NIR} + 6\text{R} - 7.5\text{B} + 1), \quad (4)$$

$$\text{GRVI} = (\text{G} - \text{R}) / (\text{G} + \text{R}), \quad (5)$$

where NDVI stands for the normalized difference vegetation index, EVI for the enhanced vegetation index (Huete et al. 2002), GRVI for the green-red vegetation index (Motohka et al. 2010), NIR is the near-infrared band (841–876 nm), R is the red band (620–670 nm), B is the blue band (459–479 nm), and G is the green band (545–565 nm) for MODIS.

Normalized difference vegetation index has been found to match well with canopy LAI at low LAI ($< 3 \text{ m}^2/\text{m}^2$; Potitthep et al. 2013, Yang et al. 2014), while EVI matched well with the maximum GPP, calculated by a process-based model which incorporates the phenology of LAI and V_{cmax} (maximum velocity of carboxylation calculated from on-tower measurements of photosynthesis/intercellular CO_2 concentration relationship by a portable photosynthesis system, LI-6400; LI-COR; Muraoka et al. 2013b). GRVI was found to be difficult to use to monitor the seasonal changes in these forest parameters, but Motohka et al. (2010) have found it to be useful to detect the date of onset (leaf expansion) and offset (leaf fall) in forests and grassland.

Ground-based optical measurements have been used to upscale spectral vegetation indices and forest canopy photosynthesis to larger areas. Muraoka et al. (2013b) applied the relationship between in situ EVI and the maximum daily GPP to EVI data of MODIS/Terra for central Japan and found that the relationship between EVI and GPP showed seasonal hysteresis, suggesting that spectral reflectance and photosynthetic capacity of a forest canopy are not always one-to-one. A similar approach has been taken by combining such spectral vegetation indices and

net ecosystem production (NEP) or net primary production (NPP) of ecosystems estimated by the eddy-covariance techniques (Xiao et al. 2004, Sims et al. 2006). But questions still remain as to whether the spectral information really expresses NEP or NPP as they are the final products of physiological processes including photosynthesis, respiration (both autotrophic and heterotrophic), and biomass accumulation, which are reflected by the large difference in the phenology derived from EVI and canopy photosynthesis across the various vegetation types of AmeriFlux sites (Shen et al. 2014b). It remains a challenge to link the spectral information from the canopy and ecological processes involved within the ecosystems.

In summary, recent technological advances have made it possible to collect tremendous data sets on plant phenology at high temporal frequency with different spatial resolutions. Although photographs and the spectral reflectance data have provided us with “visual” or “color” information that is useful for phenology observations, ecophysiological observation is also crucial to understanding the physiological mechanism underlying spectral information and the response of phenological events to the climatic conditions and their influence on photosynthetic productivity of leaves, canopies, individual plants, and vegetation (Vitasse et al. 2009, Muraoka et al. 2010, Chung et al. 2013, Yang et al. 2014).

PHENOLOGY MODELING

With knowledge gained from long-term monitoring of phenological events and improved understanding of key drivers and mechanisms, we can build phenology models to simulate the timing of phenology and to project likely future change. Models can also be used to understand how climate-induced phenological changes may affect ecosystem functions such as carbon cycling and energy flows and their feedbacks to the climate system (Richardson et al. 2013). In particular, changes in the timing of the onset and offset of the vegetation growing season have a considerable influence on the annual carbon budget in Northern Hemisphere vegetation (Piao et al. 2007, 2008, Richardson et al. 2010, Keenan et al. 2014). For example, a warming-induced advance in spring leaf emergence is suggested to increase net carbon

uptake (Piao et al. 2007, Keenan et al. 2014, Saitoh et al. 2015), while delayed autumn is found to lead to either increase (Keenan et al. 2014) or decrease in net carbon uptake (Piao et al. 2008). However, large uncertainties exist in current approaches to model spring and autumn phenology within terrestrial ecosystem models (Keenan et al. 2012, Richardson et al. 2012), of which some are used as land surface models within earth system models in an attempt to forecast future climate.

Both species-level and ecosystem-level models are limited in predictive power without the understanding of the physiological mechanisms driving phenology. They may only reflect correlative findings within specific spatiotemporal scales. A model that relies on statistical correlations between phenology and past climates may not be able to project plant phenology into new combinations of chilling experience, photoperiod, and actual thermal forcing in the future. Although some plant phenology models are based (wholly or partly) on known or hypothetical cause–effect relationships between physiological processes and environmental factors (Chuine et al. 2003, Hanninen and Kramer 2007), most rest on statistical relationships obtained from past observations because of the lack of true dose–response functions. In general, these models consider one or two development phases before leaf unfolding or flowering, endodormancy and ecodormancy. Endodormancy is induced by a decreasing photoperiod and/or temperature in the autumn and is often broken after a period of “chilling” of low temperatures (Chuine et al. 2003, Horvath 2010), with the role of photoperiod commonly unknown or unaccounted for. The ecodormancy phase begins at the end of the endodormancy phase and finishes after a period of increasing temperature (Chuine 2000, Fu et al. 2012) in spring. Based on these criteria and responses, dozens of phenology models (Chuine et al. 2003, Schaber and Badeck 2003, Fu et al. 2012, Olsson et al. 2013, Fila et al. 2014), most of them for tree species, have been developed, commonly adopting the following general function (see Chuine et al. 2003 for a list of species-level models):

$$t_n \text{ such that } S_{n,t} = \sum_{t_{n-1}}^{t_n} R_{n,t}(Z) = S_n^* \quad (6)$$

where t_n and t_{n-1} are the dates at the end of development phases n and $n-1$, respectively, $R_{n,t}$ is the rate of development in phase n on day t , Z is the environmental factor such as temperature or photoperiod, $S_{n,t}$ is the state of development in phase n on day t , and S_n^* is the critical state to finish the development phase (Chuine et al. 2003). One may take a chilling-forcing model for leaf unfolding, for example, with $S_{1,t}$ representing the sum of chilling (endodormancy phase) and $S_{2,t}$ being the accumulative degree-days (ecodormancy phase). To specify Eq. 6 for timing phenology, one needs to determine the number of phases, parameters and functional type of $R_{n,t}(Z)$, and the critical value of S_n^* . For example, in a chilling-forcing model, one needs to determine the period, the functional type of development, base temperature, and the critical value for chilling sum (Chuine 2000). For a given species and in a given location, such a task is possible, with the predicted phenological timing differing from observations by a few days only (e.g., Jeong et al. 2013), if the observations and knowledge of physiological processes related to chilling and forcing are sufficient and if photoperiod does not matter. However, in the real world, such knowledge and observation are usually insufficient for most species and thus effective phenological models for these species are lacking. We are still not clear about the physiological basis of the endodormancy and the transition to ecodormancy related to chilling experience. In a recent study based on 490 species, only about 20% showed a relationship between phenology and winter temperature in regression analysis (Cook et al. 2012). We can only infer that for the other 80%, either chilling is not required, or the chilling requirement is not met by the measures of temperature employed for defining chilling.

The lack of species-level knowledge and observation data further leads to difficulty in developing vegetation phenology models at ecosystem or community scales, particularly for nonwoody vegetation types, although those models are essential in some terrestrial ecosystem models that are embedded in earth system models. Hence, most of the current phenology models have the same structure and similar functional type to the species-level ones to describe the effect of environmental drivers (Botta et al. 2000, Krinner et al. 2005, Knorr et al. 2010, Migliavacca et al. 2012, Richardson et al.

2012, Yang et al. 2012) at the ecosystem scale where vegetation types are derived from satellite data (Botta et al. 2000). Those vegetation phenology models are often driven by meteorological data to simulate seasonal leafing dynamics such as LAI (Richardson et al. 2012). Such simulations, however, show large biases and only explain a limited fraction of interannual variation in observed phenological dates although some could perform better than others for a certain vegetation type, which further leads to poor prediction of GPP (Lafont et al. 2012, Richardson et al. 2012). Such a model would firstly suffer from the large uncertainties in the satellite-derived (statistical) phenology data (Botta et al. 2000, Picard et al. 2005, Cong et al. 2012), particularly for the nonforested vegetation at the middle and high latitude (Cao et al. 2015) and the tropical forest of which the phenology is difficult to capture by satellite data.

Another challenge to developing ecosystem-scale phenology models emerges from the difference in the phenology of different species that assemble a community. As we described earlier, different functional groups and successional

stages of species have their own strategies in response to environmental cues. It is difficult to aggregate all these responses into a single model to simulate vegetation phenology at ecosystem or regional scales. Even though we may use the same model structure for ecosystem-scale phenology as the species-scale (taking the chilling-forcing model for example), there are still several challenges, including selecting an aggregated response type, threshold temperatures above or below which forcing or chilling takes place, time periods for calculating the status of chilling and forcing, temperature data to be used (i.e., daily mean, maximum, minimum, or daytime mean temperature), and critical status of chilling and forcing. It is more complicated if we consider different responses to the same environmental factor among various species and multiple environmental factors and if the species composition of a community evolves with long-term climate change. Therefore, it is challenging to develop vegetation phenology models by integrating the phenology response of all the coexisting species within a community. However, recent advances

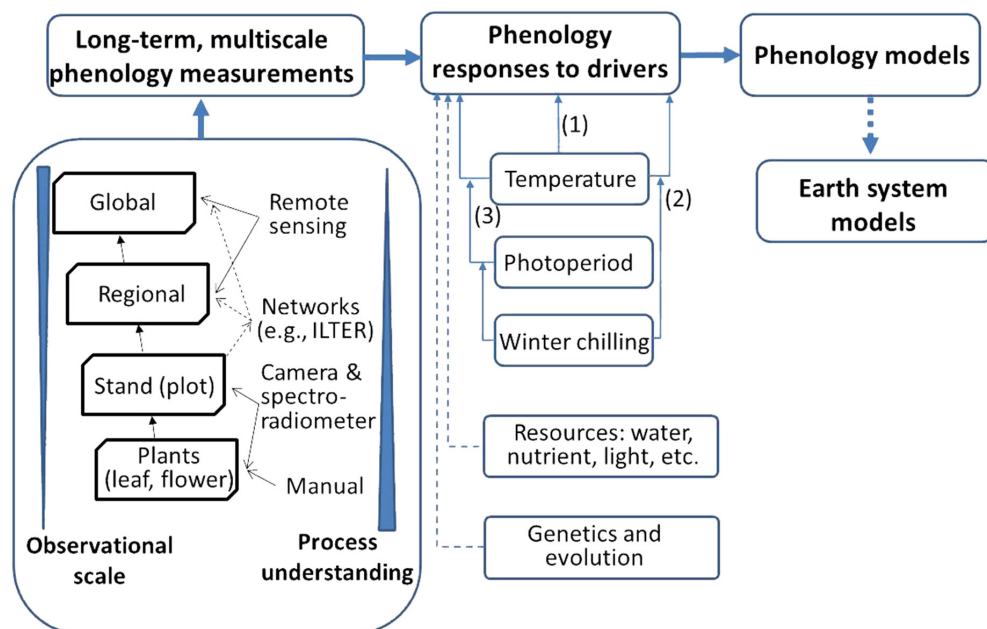


Fig. 3. Integrating long-term, cross-scale phenology measurements and modeling to improve understanding of phenology, its response to climate change, and underlying physiological mechanisms. Arrowed lines indicate drivers and informational inputs; dashes indicate underdeveloped. Hierarchical drivers of temperature, chilling, and photoperiod indicate that (1) temperature alone, (2) temperature + chilling, or (3) temperature + photoperiod + chilling drive phenology.

in monitoring methods and cumulative phenology data from long-term research networks are paving the way for developing vegetation phenology models at large scales as a critical component of earth system models (Basler 2016).

CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

With an ever-increasing array of techniques for observing phenology at a range of different scales, phenology research has entered a new stage that needs to integrate all relevant disciplines and take advantage of new technologies and long-term data collection. We emphasize that while photographs and spectral data are important to phenological research, acquiring better understanding of the physiological mechanisms governing phenology is essential. When mechanistic developments match advances of observation techniques, we will be able to not only understand drivers of phenological change at multiple scales, but also greatly improve predictive modeling capabilities. Fig. 3 summarizes a framework of integrated phenological measurements, mechanisms, and modeling to advance our understanding of phenology and knowledge gaps (dashed lines) for further research.

We recommend more studies to advance understanding of the mechanisms governing phenology and to disentangle the interacting effects of temperature, photoperiod, and winter chilling, as well as genetic controls and evolutionary dynamics for individual species. In addition to this essential ecophysiological understanding, we should also address consequences of phenological shifts for ecological processes at multiple scales, their geographical variation such as along altitudinal and latitudinal gradients, the teleconnection of ecological functions (Heffernan et al. 2014), and the influence of, and response to, climate change. Further, standardization and interoperability of recent technologies in observing phenology over long temporal scales, such as using digital cameras and spectroradiometers, from plot to regional scales are critically needed.

International research networks such as ILTER can play an important role in standardizing phenology research protocols. Automatic repeat cameras that are able to conveniently and continuously record phenology should be installed in networked sites for long-term monitoring

of phenology. These cameras should be complemented by spectroradiometers to monitor leaf- and canopy-scale ecophysiology to capture additional physiological variables other than color information alone. The development of low-cost hyperspectral cameras along with new spectral indices and new devices to capture solar-induced fluorescence to track in situ vegetation activities is strongly recommended. As these observation systems are connected as a network, they can provide phenological observations across multiple scales, from canopy, landscape, regional to the global. Such networks that also offer long-term human-collected data about phenological events are a rich basis for cross-scale phenological data synthesis.

Given the opportunity of collecting unprecedented phenology data with advanced technologies, we envision a breakthrough in process-based phenology modeling, once biological drivers, dose-response functions, or threshold functions are available, rather than building solely upon correlative statistics based on past observations. The phenology models will need to account for the rate of microevolutionary adjustments of genotypic phenology controls. The current conspecific variability in phenology should not be simply considered “noise” but rather the starting point of evolutionary selection within subpopulations. Our understanding of individual species’ phenological strategies in response to a changing environment remains incomplete and thus limits our ability to develop robust phenology models at the ecosystem scale. With these advancements, phenology models would be better parameterized and represented within earth system models.

ACKNOWLEDGMENTS

JT was partially supported by the U.S. National Science Foundation grants PLR-1417763, DBI-959333, and AGS-1005663 and the University of Chicago and the MBL Lillie Research Innovation Award. HM thanks “PEN” developmental team and colleagues at the Takayama site and JALTER, especially Nagai, Nasahara, Saitoh, Noda, Nakaji, and Hiura, and his research has been supported by NEXT Program and KAKENHI (MEXT, Japan). MS is partly supported by a fund from the National Science Foundation of China (grant 41571103). SJT was supported by an NERC grant NE/J02080X/1. We thank comments and edits by two anonymous reviewers, Kristin Vanderbilt, Mary Heskell, and

Thomas Parker in improving an earlier version of this manuscript. The authors declare no conflict of interest.

LITERATURE CITED

- Allstadt, A. J., S. J. Vavrus, P. J. Heglund, A. M. Pidgeon, W. E. Thogmartin, and V. C. Radeloff. 2015. Spring plant phenology and false springs in the conterminous US during the 21st century. *Environmental Research Letters* 10:104008. <http://dx.doi.org/10.1088/1748-9326/10/10/104008>.
- Anderson, M. C. 1964. Studies of the woodland light climate. 1. The photographic computation of light conditions. *Journal of Ecology* 52:27–41.
- Asner, G. P., and R. E. Martin. 2008. Spectral and chemical analysis of tropical forests: scaling from leaf to canopy levels. *Remote Sensing of Environment* 112:3958–3970.
- Asner, G. P., R. E. Martin, R. Tupayachi, C. B. Anderson, F. Sinca, L. Carranza-Jimenez, and P. Martinez. 2014. Amazonian functional diversity from forest canopy chemical assembly. *Proceedings of the National Academy of Sciences USA* 111:5604–5609.
- Baker, N. R. 2008. Chlorophyll fluorescence: a probe of photosynthesis in vivo. *Annual Review of Plant Biology* 59:89–113.
- Basler, D. 2016. Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central Europe. *Agricultural and Forest Meteorology* 217:10–21.
- Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- Botta, A., N. Viovy, P. Ciais, P. Friedlingstein, and P. Monfray. 2000. A global prognostic scheme of leaf onset using satellite data. *Global Change Biology* 6:709–725.
- Cao, R. Y., J. Chen, M. G. Shen, and Y. H. Tang. 2015. An improved logistic method for detecting spring vegetation phenology in grasslands from MODIS EVI time-series data. *Agricultural and Forest Meteorology* 200:9–20.
- Chazdon, R. L., and C. B. Field. 1987. Photographic estimation of photosynthetically active radiation – evaluation of a computerized technique. *Oecologia* 73:525–532.
- Chew, Y. H., A. M. Wilczek, M. Williams, S. M. Welch, J. Schmitt, and K. J. Halliday. 2012. An augmented *Arabidopsis* phenology model reveals seasonal temperature control of flowering time. *New Phytologist* 194:654–665.
- Chuine, I. 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* 207:337–347.
- Chuine, I., K. Kramer, and H. Hänninen. 2003. Plant development models. Pages 217–235 in M. Schwartz, editor. *Phenology: an integrative environmental science*. Springer, Dordrecht, The Netherlands.
- Chung, H., H. Muraoka, M. Nakamura, S. Han, O. Muller, and Y. Son. 2013. Experimental warming studies on tree species and forest ecosystems: a literature review. *Journal of Plant Research* 126:447–460.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* 22:357–365.
- Cong, N., S. L. Piao, A. P. Chen, X. H. Wang, X. Lin, S. P. Chen, S. J. Han, G. S. Zhou, and X. P. Zhang. 2012. Spring vegetation green-up date in China inferred from SPOT NDVI data: a multiple model analysis. *Agricultural and Forest Meteorology* 165:104–113.
- Cook, B. I., E. M. Wolkovich, and C. Parmesan. 2012. Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences USA* 109:9000–9005.
- Craine, J. M., E. M. Wolkovich, E. G. Towne, and S. W. Kembel. 2012. Flowering phenology as a functional trait in a tallgrass prairie. *New Phytologist* 193:673–682.
- Daumard, F., S. Champagne, A. Fournier, Y. Goulas, A. Ounis, J. F. Hanocq, and I. Moya. 2010. A field platform for continuous measurement of canopy fluorescence. *IEEE Transactions on Geoscience and Remote Sensing* 48:3358–3368.
- Defila, C., and B. Clot. 2001. Phytophenological trends in Switzerland. *International Journal of Biometeorology* 45:203–207.
- Fila, G., M. Gardiman, P. Belvini, F. Meggio, and A. Pitacco. 2014. A comparison of different modelling solutions for studying grapevine phenology under present and future climate scenarios. *Agricultural and Forest Meteorology* 195:192–205.
- Fisher, J. I., and J. F. Mustard. 2007. Cross-scalar satellite phenology from ground, Landsat, and MODIS data. *Remote Sensing of Environment* 109:261–273.
- Fu, Y. S. H., M. Campioli, M. Van Oijen, G. Deckmyn, and I. A. Janssens. 2012. Bayesian comparison of six different temperature-based budburst models for four temperate tree species. *Ecological Modelling* 230:92–100.
- Gitelson, A. A., Y. Gritz, and M. N. Merzlyak. 2003. Relationships between leaf chlorophyll content and spectral reflectance and algorithms for non-destructive chlorophyll assessment in higher plant leaves. *Journal of Plant Physiology* 160:271–282.
- Guanter, L., C. Frankenberg, A. Dudhia, P. E. Lewis, J. Gomez-Dans, A. Kuze, H. Suto, and R. G. Grainger. 2012. Retrieval and global assessment of terrestrial chlorophyll fluorescence from GOSAT space measurements. *Remote Sensing of Environment* 121:236–251.

- Guanter, L., M. Rossini, R. Colombo, M. Meroni, C. Frankenberg, J. E. Lee, and J. Joiner. 2013. Using field spectroscopy to assess the potential of statistical approaches for the retrieval of sun-induced chlorophyll fluorescence from ground and space. *Remote Sensing of Environment* 133:52–61.
- Hanninen, H., and K. Kramer. 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fennica* 41:167–205.
- Heffernan, J. B., et al. 2014. Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Frontiers in Ecology and the Environment* 12:5–14.
- Hilker, T., et al. 2010. Remote sensing of photosynthetic light-use efficiency across two forested biomes: spatial scaling. *Remote Sensing of Environment* 114:2863–2874.
- Hirose, T. 2005. Development of the Monsi-Saeki theory on canopy structure and function. *Annals of Botany* 95:483–494.
- Homolova, L., Z. Maenovskiy, J. G. P. W. Clevers, G. Garcia-Santos, and M. E. Schaepman. 2013. Review of optical-based remote sensing for plant trait mapping. *Ecological Complexity* 15:1–16.
- Horvath, D. 2010. Bud dormancy and growth. Pages 53–70 in E. C. Pua and M. R. Davey, editors. *Plant developmental biology: biotechnological perspectives*. Springer, Berlin, Germany.
- Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83:195–213.
- Ide, R., and H. Oguma. 2010. Use of digital cameras for phenological observations. *Ecological Informatics* 5:339–347.
- Janick, J. 2005. The origin of fruits, fruit growing and fruit breeding. *Plant Breeding Reviews* 25:255–320.
- Jeong, S.-J., D. Medvigy, E. Shevliakova, and S. Malyshev. 2013. Predicting changes in temperate forest budburst using continental-scale observations and models. *Geophysical Research Letters* 40:359–364.
- Joiner, J., L. Guanter, R. Lindstrot, M. Voigt, A. P. Vasilkov, E. M. Middleton, K. F. Huemmrich, Y. Yoshida, and C. Frankenberg. 2013. Global monitoring of terrestrial chlorophyll fluorescence from moderate-spectral-resolution near-infrared satellite measurements: methodology, simulations, and application to GOME-2. *Atmospheric Measurement Techniques* 6:2803–2823.
- Joiner, J., Y. Yoshida, A. P. Vasilkov, Y. Yoshida, L. A. Corp, and E. M. Middleton. 2011. First observations of global and seasonal terrestrial chlorophyll fluorescence from space. *Biogeosciences* 8:637–651.
- Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Copin, M. Weiss, and F. Baret. 2004. Review of methods for in situ leaf area index determination—Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology* 121:19–35.
- Keenan, T. F., et al. 2012. Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO₂ exchange. *Global Change Biology* 18:1971–1987.
- Keenan, T. F., et al. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* 4:598–604.
- Knorr, W., T. Kaminski, M. Scholze, N. Gobron, B. Pinty, R. Giering, and P. P. Mathieu. 2010. Carbon cycle data assimilation with a generic phenology model. *Journal of Geophysical Research-Biogeosciences* 115:G04017. <http://dx.doi.org/10.1029/2009JG001119>
- Körner, C., and D. Basler. 2010. Phenology under global warming. *Science* 327:1461–1462.
- Körner, C., D. Basler, G. Hoch, C. Kollas, A. Lenz, C. F. Randin, Y. Vitasse, and N. E. Zimmermann. 2016. Where, why and how? Explaining the low temperature range limits of temperate tree species. *Journal of Ecology* 104:1076–1088.
- Krinner, G., N. Viovy, N. de Noblet-Ducoudre, J. Ogee, J. Polcher, P. Friedlingstein, P. Ciais, S. Sitch, and I. C. Prentice. 2005. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles* 19:GB1015. <http://dx.doi.org/10.1029/2003GB002199>
- Lafont, S., Y. Zhao, J. C. Calvet, P. Peylin, P. Ciais, F. Maignan, and M. Weiss. 2012. Modelling LAI, surface water and carbon fluxes at high-resolution over France: comparison of ISBA-A-gs and ORCHIDEE. *Biogeosciences* 9:439–456.
- Larcher, W. 2006. Altitudinal variation in flowering time of lilac (*Syringa vulgaris* L.) in the Alps in relation to temperatures. *Sitzungsber Abt. I* 212:3–18.
- Lee, J. E., et al. 2013. Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll fluorescence. *Proceedings of Royal Society B* 280:20130171.
- Lenz, A., Y. Vitasse, G. Hoch, and C. Körner. 2014. Growth and carbon relations of temperate deciduous tree species at their upper elevation range limit. *Journal of Ecology* 102:1537–1548.
- Liu, Z., H. Hu, H. Yu, X. Yang, H. Yang, C. Ruan, Y. Wang, and J. Tang. 2015. Relationship between leaf physiologic traits and canopy color indices during the leaf expansion period in an oak forest. *Ecosphere* 6:259.
- Markwell, J., J. C. Osterman, and J. L. Mitchell. 1995. Calibration of the Minolta SPAD-502 leaf chlorophyll meter. *Photosynthesis Research* 46:467–472.
- Meroni, M., M. Rossini, L. Guanter, L. Alonso, U. Rascher, R. Colombo, and J. Moreno. 2009. Remote sensing of solar-induced chlorophyll

- fluorescence: review of methods and applications. *Remote Sensing of Environment* 113:2037–2051.
- Migliavacca, M., O. Sonnentag, T. F. Keenan, A. Cescatti, J. O’Keefe, and A. D. Richardson. 2012. On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences* 9:2063–2083.
- Miller-Rushing, A. J., R. B. Primack, D. Primack, and S. Mukunda. 2006. Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany* 93:1667–1674.
- Monsi, M., and T. Saeki. 2005. On the factor light in plant communities and its importance for matter production. *Annals of Botany* 95:549–567.
- Morisette, J. T., et al. 2009. Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment* 7:253–260.
- Motohka, T., K. N. Nasahara, H. Oguma, and S. Tsuchida. 2010. Applicability of green-red vegetation index for remote sensing of vegetation phenology. *Remote Sensing* 2:2369–2387.
- Muraoka, H., and H. Koizumi. 2009. Satellite Ecology (SATECO) – linking ecology, remote sensing and micrometeorology, from plot to regional scale, for the study of ecosystem structure and function. *Journal of Plant Research* 122:3–20.
- Muraoka, H., R. Ishii, S. Nagai, R. Suzuki, T. Motohka, H. Noda, M. Hirota, K. N. Nasahara, H. Oguma, and K. Muramatsu. 2013a. Linking remote sensing and in situ ecosystem/biodiversity observations by “Satellite Ecology”. Pages 277–308 in S. E. A. Nakano, editor. *The biodiversity observation network in the Asia-Pacific region: toward further development of monitoring*. Ecological Research Monographs. Springer, New York, New York, USA.
- Muraoka, H., and H. Koizumi. 2005. Photosynthetic and structural characteristics of canopy and shrub trees in a cool-temperate deciduous broadleaved forest: implication to the ecosystem carbon gain. *Agricultural and Forest Meteorology* 134:39–59.
- Muraoka, H., H. M. Noda, S. Nagai, T. Motohka, T. M. Saitoh, K. N. Nasahara, and N. Saigusa. 2013b. Spectral vegetation indices as the indicator of canopy photosynthetic productivity in a deciduous broadleaf forest. *Journal of Plant Ecology* 6:393–407.
- Muraoka, H., N. Saigusa, K. N. Nasahara, H. Noda, J. Yoshino, T. M. Saitoh, S. Nagai, S. Murayama, and H. Koizumi. 2010. Effects of seasonal and interannual variations in leaf photosynthesis and canopy leaf area index on gross primary production of a cool-temperate deciduous broadleaf forest in Takayama, Japan. *Journal of Plant Research* 123:563–576.
- Nagai, S., T. Maeda, M. Gamo, H. Muraoka, R. Suzuki, and K. N. Nasahara. 2011. Using digital camera images to detect canopy condition of deciduous broad-leaved trees. *Plant Ecology & Diversity* 4:79–89.
- Nagai, S., S. Yoshitake, T. Inoue, R. Suzuki, H. Muraoka, K. N. Nasahara, and T. M. Saitoh. 2014. Year-to-year blooming phenology observation using time-lapse digital camera images. *Journal of Agricultural Meteorology* 70:163–170.
- Nakaji, T., R. Ide, H. Oguma, N. Saigusa, and Y. Fujinuma. 2007. Utility of spectral vegetation index for estimation of gross CO₂ flux under varied sky conditions. *Remote Sensing of Environment* 109:274–284.
- Nakaji, T., R. Ide, K. Takagi, Y. Kosugi, S. Ohkubo, K. N. Nasahara, N. Saigusa, and H. Oguma. 2008. Utility of spectral vegetation indices for estimation of light conversion efficiency in coniferous forests in Japan. *Agricultural and Forest Meteorology* 148:776–787.
- Nasahara, K. N., and S. Nagai. 2015. Review: Development of an in situ observation network for terrestrial ecological remote sensing: the Phenological Eyes Network (PEN). *Ecological Research* 30:211–223.
- Nijland, W., R. de Jong, S. M. de Jong, M. A. Wulder, C. W. Bater, and N. C. Coops. 2014. Monitoring plant condition and phenology using infrared sensitive consumer grade digital cameras. *Agricultural and Forest Meteorology* 184:98–106.
- Noda, H. M., H. Muraoka, K. N. Nasahara, N. Saigusa, S. Murayama, and H. Koizumi. 2015. Phenology of leaf morphological, photosynthetic, and nitrogen use characteristics of canopy trees in a cool-temperate deciduous broadleaf forest at Takayama, central Japan. *Ecological Research* 30:247–266.
- Olsson, C., K. Bolmgren, J. Lindstrom, and A. M. Jonsen. 2013. Performance of tree phenology models along a bioclimatic gradient in Sweden. *Ecological Modelling* 266:103–117.
- Pau, S., E. M. Wolkovich, B. I. Cook, T. J. Davies, N. J. B. Kraft, K. Bolmgren, J. L. Betancourt, and E. E. Cleland. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* 17:3633–3643.
- Pearcy, R. W. 1989. Radiation and light measurements. Pages 97–116 in R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. *Plant physiological ecology: field methods and instrumentation*. Chapman & Hall, Boca Raton, Florida, USA.
- Penuelas, J., T. Rutishauser, and I. Filella. 2009. Phenology feedbacks on climate change. *Science* 324: 887–888.
- Pianka, E. R. 1970. On r- and K-selection. *American Naturalist* 104:592–597.

- Piao, S. L., et al. 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* 451:49–52.
- Piao, S. L., et al. 2015. Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature Communications* 6:6911. <http://dx.doi.org/10.1038/ncomms7911>
- Piao, S. L., J. Y. Fang, L. M. Zhou, Q. H. Guo, M. Henderson, W. Ji, Y. Li, and S. Tao. 2003. Interannual variations of monthly and seasonal normalized difference vegetation index (NDVI) in China from 1982 to 1999. *Journal of Geophysical Research-Atmospheres* 108:4401. <http://dx.doi.org/10.1029/2002JD002848>
- Piao, S. L., P. Friedlingstein, P. Ciais, N. Viovy, and J. Demarty. 2007. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochemical Cycles* 21:GB3018. <http://dx.doi.org/10.1029/2006GB002888>
- Picard, G., S. Quegan, N. Delbart, M. R. Lomas, T. Le Toan, and F. I. Woodward. 2005. Bud-burst modelling in Siberia and its impact on quantifying the carbon budget. *Global Change Biology* 11:2164–2176.
- Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* 191:926–941.
- Porra, R. J., W. A. Thompson, and P. E. Kriedemann. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophyll a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica et Biophysica Acta* 975:384–394.
- Potitthep, S., S. Nagai, K. N. Nasahara, H. Muraoka, and R. Suzuki. 2013. Two separate periods of the LAI-VIs relationships using in situ measurements in a deciduous broadleaf forest. *Agricultural and Forest Meteorology* 169:148–155.
- Richardson, A. D., A. S. Bailey, E. G. Denny, C. W. Martin, and J. O'Keefe. 2006. Phenology of a northern hardwood forest canopy. *Global Change Biology* 12:1174–1188.
- Richardson, A. D., B. H. Braswell, D. Y. Hollinger, J. P. Jenkins, and S. V. Ollinger. 2009. Near-surface remote sensing of spatial and temporal variation in canopy phenology. *Ecological Applications* 19:1417–1428.
- Richardson, A. D., et al. 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B* 365:3227–3246.
- Richardson, A. D., et al. 2012. Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program site synthesis. *Global Change Biology* 18:566–584.
- Richardson, A. D., J. P. Jenkins, B. H. Braswell, D. Y. Hollinger, S. V. Ollinger, and M. L. Smith. 2007. Use of digital webcam images to track spring green-up in a deciduous broadleaf forest. *Oecologia* 152:323–334.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.
- Rollinson, C. R., and M. W. Kaye. 2012. Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. *Global Change Biology* 18:1108–1116.
- Saitoh, T. M., S. Nagai, N. Saigusa, H. Kobayashi, R. Suzuki, K. N. Nasahara, and H. Muraoka. 2012. Assessing the use of camera-based indices for characterizing canopy phenology in relation to gross primary production in a deciduous broad-leaved and an evergreen coniferous forest in Japan. *Ecological Informatics* 11:45–54.
- Saitoh, T. M., S. Nagai, J. Yoshino, H. Kondo, I. Tamagawa, and H. Muraoka. 2015. Effects of canopy phenology on deciduous overstory and evergreen understory carbon budgets in a cool-temperate forest ecosystem under ongoing climate change. *Ecological Research* 30:267–277.
- Saleska, S., K. Didan, A. Huete, and H. R. Da Rocha. 2007. Amazon forests green-up during 2005 drought. *Science* 318:612.
- Satake, A., T. Kawagoe, Y. Saburi, Y. Chiba, G. Sakurai, and H. Kudoh. 2013. Forecasting flowering phenology under climate warming by modelling the regulatory dynamics of flowering-time genes. *Nature Communications* 4:2303. <http://dx.doi.org/10.1038/ncomms3303>
- Schaber, J., and F. W. Badeck. 2003. Physiology-based phenology models for forest tree species in Germany. *International Journal of Biometeorology* 47:193–201.
- Schwartz, M. D., and J. M. Hanes. 2010. Continental-scale phenology: warming and chilling. *International Journal of Climatology* 30:1595–1598.
- Shen, M. G., et al. 2014a. Earlier-season vegetation has greater temperature sensitivity of spring phenology in Northern Hemisphere. *PLoS ONE* 9:e88178. <http://dx.doi.org/10.1371/journal.pone.0088178>
- Shen, M. G., S. L. Piao, N. Cong, G. X. Zhang, and I. A. Jassens. 2015. Precipitation impacts on vegetation spring phenology on the Tibetan Plateau. *Global Change Biology* 21:3647–3656.
- Shen, M. G., Y. H. Tang, A. R. Desai, C. Gough, and J. Chen. 2014b. Can EVI-derived land-surface phenology be used as a surrogate for phenology

- of canopy photosynthesis? *International Journal of Remote Sensing* 35:1162–1174.
- Sims, D. A., et al. 2006. On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. *Journal of Geophysical Research-Biogeosciences* 111:G04015. <http://dx.doi.org/10.1029/2006JG000162>
- Sonnentag, O., K. Hufkens, C. Teshera-Sterne, A. M. Young, M. Friedl, B. H. Braswell, T. Milliman, J. O'Keefe, and A. D. Richardson. 2012. Digital repeat photography for phenological research in forest ecosystems. *Agricultural and Forest Meteorology* 152:159–177.
- Stagakis, S., N. Markos, O. Sykioti, and A. Kyparissis. 2014. Tracking seasonal changes of leaf and canopy light use efficiency in a *Phlomis fruticosa* Mediterranean ecosystem using field measurements and multi-angular satellite hyperspectral imagery. *ISPRS Journal of Photogrammetry and Remote Sensing* 97:138–151.
- Steltzer, H., and E. Post. 2009. Seasons and life cycles. *Science* 324:886–887.
- Tang, J., P. V. Bolstad, A. R. Desai, J. G. Martin, B. D. Cook, K. J. Davis, and E. V. Carey. 2008. Ecosystem respiration and its components in an old-growth northern forest. *Agricultural and Forest Meteorology* 148:171–185.
- Verhoef, W. 1984. Light-scattering by leaf layers with application to canopy reflectance modeling: the sail model. *Remote Sensing of Environment* 16:125–141.
- Visser, M. E., and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society B* 268:289–294.
- Vitasse, Y. 2013. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist* 198:149–155.
- Vitasse, Y., S. Delzon, E. Dufrene, J. Y. Pontailler, J. M. Louvet, A. Kremer, and R. Michalet. 2009. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology* 149:735–744.
- Vitasse, Y., C. Francois, N. Delpierre, E. Dufrene, A. Kremer, I. Chuine, and S. Delzon. 2011. Assessing the effects of climate change on the phenology of European temperate trees. *Agricultural and Forest Meteorology* 151:969–980.
- Vitasse, Y., A. Lenz, G. Hoch, and C. Körner. 2014a. Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. *Journal of Ecology* 102:981–988.
- Vitasse, Y., A. Lenz, and C. Körner. 2014b. The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science*. <http://dx.doi.org/10.3389/fpls.2014.00541>
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Wilczek, A. M., et al. 2009. Effects of genetic perturbation on seasonal life history plasticity. *Science* 323:930–934.
- Wingate, L., et al. 2015. Interpreting canopy development and physiology using the EUROPhen camera network at flux sites. *Biogeosciences Discussion* 12:7979–8034.
- Wolkovich, E. M., B. I. Cook, and T. J. Davies. 2014. Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. *New Phytologist* 201:1156–1162.
- Xiao, X. M., Q. Y. Zhang, B. Braswell, S. Urbanski, S. Boles, S. Wofsy, M. Berrien, and D. Ojima. 2004. Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data. *Remote Sensing of Environment* 91:256–270.
- Xu, L., et al. 2013. Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change* 3:581–586.
- Yang, X., J. F. Mustard, J. W. Tang, and H. Xu. 2012. Regional-scale phenology modeling based on meteorological records and remote sensing observations. *Journal of Geophysical Research-Biogeosciences* 117:G03029. <http://dx.doi.org/10.1029/2012JG001977>
- Yang, X., J. Tang, and J. Mustard. 2014. Beyond leaf color: comparing camera-based phenological metrics with leaf biochemical, biophysical and spectral properties throughout the growing season of a temperate deciduous forest. *Journal of Geophysical Research-Biogeosciences* 119:181–191.
- Yang, X., J. W. Tang, J. F. Mustard, J. E. Lee, M. Rossini, J. Joiner, J. W. Munger, A. Kornfeld, and A. D. Richardson. 2015. Solar-induced chlorophyll fluorescence that correlates with canopy photosynthesis on diurnal and seasonal scales in a temperate deciduous forest. *Geophysical Research Letters* 42:2977–2987.
- Zhang, X. Y., M. A. Friedl, C. B. Schaaf, A. H. Strahler, J. C. F. Hodges, F. Gao, B. C. Reed, and A. Huete. 2003. Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment* 84:471–475.